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1 Local factors mediate the response of biodiversity to land use on two African mountains

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20 Abstract

21 Land-use change is the single biggest driver of biodiversity loss in the tropics. Broad-scale biodiversity models
22 can be useful tools to inform policy-makers and conservationists of the likely response of species to
23 anthropogenic pressures, including land-use change. However, such models generalize biodiversity responses
24 across wide areas and many taxa, potentially missing important characteristics of particular sites or clades.
25 Comparisons of broad-scale models with independently collected field data can help us understand the local
26 factors that mediate broad-scale responses.

27 We collected bird occurrence and abundance data along two elevational transects in Mount Kilimanjaro,
28 Tanzania and the Taita Hills, Kenya. We estimated the local response to land use and compared our estimates
29 with modelled responses based on a broad-scale, but fine-resolution, database of many different taxa across
30 Africa. To identify the local factors mediating responses to land use, we compared environmental and species
31 assemblage information between sites in the local and broad-scale data sets.

32 Bird species richness and abundance responses to land use in the independent data followed similar
33 trends as suggested by the broad-scale model, but the broad-scale land-use classification was too coarse to
34 capture fully the variability introduced by local agricultural management practices. A comparison of assemblage

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characteristics showed that the sites on Kilimanjaro and the Taita Hills had higher proportions of forest specialists in croplands compared to the Africa-wide average. Local human population density, forest cover and vegetation greenness also differed significantly between the local and broad-scale datasets. Broad-scale models including those variables performed better, but still could not accurately predict the magnitude of local species responses to most land uses, probably because local features of the land management are still missed.

Overall, our study demonstrates that local factors mediate biodiversity responses to land use and cautions against applying broad-scale models to local contexts without prior knowledge of which broad-scale factors are locally relevant.

Keywords:

Modelling; Birds; Eastern Arc Mountains; Homegardens; Kilimanjaro; PREDICTS; Taita Hills;

46 **Introduction**

47 Humanity drives global biodiversity decline in many different ways (Butchart et al. 2010). Among the different
48 pressures, anthropogenic land-use change has been shown to have the most severe impact on terrestrial biodiversity (Foley
49 et al. 2005; Jetz et al. 2007; Gibson et al. 2011). A change in land use might greatly reduce the amount or quality of habitat
50 available to species, or contribute to landscape fragmentation resulting in declining species abundance and/or local
51 extinctions (Brooks et al. 2002). Therefore it is of particular interest to understand how assemblages of species respond
52 to land use, and if they can persist in a human-modified landscape (Gardner et al. 2007). Broad-scale statistical models
53 are increasingly employed to predict the response of species assemblages to land use (Loh et al. 2005; Scholes and Biggs
54 2005; Alkemade et al. 2009; Newbold et al. 2014a; Newbold et al. 2015). Such models can be based on data from many
55 different taxonomic groups, and can inform policy-makers about biodiversity trends and influence ongoing international
56 debates about relevant mitigation schemes (Pereira et al. 2010; Leadley et al. 2014; CBD 2014). However, in generalising
57 across a broad area, such models likely miss local factors that mediate species' response to land use.

58 Most broad-scale models employ a coarse land-use classification scheme (eg. Scholes and Biggs 2005; Alkemade
59 et al. 2009; Newbold et al. 2014a; Newbold et al. 2015) that cannot capture the full variability of local land-use systems,
60 often missing important land-use categories such as agroforestry (Scholes and Biggs 2005; Newbold et al. 2015). Others
61 ignore the differential responses of taxonomic groups (Alkemade et al. 2009), which can be important (e.g., Gibson et al.
62 2011; Murphy and Romanuk 2014; Newbold et al. 2014a). Some broad-scale models of local species richness and
63 abundance have found environmental variables such as land-use intensity, human population density and metrics derived
64 from vegetation-greenness data to be influential (Newbold et al. 2014a; De Palma et al. 2015). It is however unclear if
65 the inclusion of these variables is relevant in understanding how the local environment mediates biodiversity responses
66 to land use. Similarly it has been shown that functional characteristics can help explain species' varying responses to land
67 use on a broad scale (Owens and Bennett 2000; Flynn et al. 2009; Newbold et al. 2013; De Palma et al. 2015), but to our
68 knowledge no previous studies have evaluated whether those responses are consistent in a local context. Comparing
69 estimates derived from broad-scale models with local independent data, where the detailed environmental conditions are
70 known and taken into account, could help to identify some of the important local factors that mediate biodiversity
71 responses to land use and ultimately provide insight on how to improve the applicability of broad-scale models.

72 Addressing the question of how biodiversity responds to land use is especially important in sub-Saharan Africa,
73 where the congruent and patchy distribution of both biodiversity and human population leads to a high risk of biodiversity
74 loss (Balmford et al. 2001; Burgess et al. 2007a; Pfeifer et al. 2012). In this study we investigated biodiversity responses

to land use in two study areas in east Africa each with different geological, evolutionary and land-use history. We explicitly test if (1) the response of avian diversity to land use is different in those study areas compared to a taxonomically and geographically broad Africa-wide model of local biodiversity responses to land use, (2) investigate potential explanations for any mismatches using remote-sensed data and information on species' ecological characteristics and threat status, to identify the local factors that mediate the local response of biodiversity to land use; and (3) make recommendations for additional factors to be included in broad-scale biodiversity models and sampling choices for biodiversity surveys.

Methods

Assemblage composition data

To generate broad-scale estimates of how local species richness and abundance respond to land use, we used the database of the **Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS)** project (Hudson et al. 2014; www.predicts.org.uk). We used only the data sources for Africa (extracted 28/07/2014, see Table SI 1) with land use in each site classified as primary vegetation (1285 sites), secondary vegetation (485), plantation forest (441), cropland (612) and urban (33) habitat (see Hudson et al. 2014 for definitions). Additionally, we also used the information on land-use intensity according to the classification developed by the PREDICTS Project, which combines information on management intensity and proportion of each site impacted (SI Table 2; Hudson et al. 2014). This classification was used so that different land uses could be compared across the different studies, both in the broad-scale dataset and the independent field data, and necessarily means that some of the variability in land-use systems is omitted.

We collected fine-scale field data for birds (herein called 'independent data') along two transects on the southern slopes of Mount Kilimanjaro, Tanzania and the Taita Hills, Kenya (Figure 1). Both landscapes are known for their long history of human modification (Conte 2010; Heckmann et al. 2014), while having a contrasting geological age (~ 30 mil. years for Taita compared to ~2 mil. years for Kilimanjaro, see Platts et al. 2011), and each has different sets of endemic species (Hemp 2006a; Burgess et al. 2007b). Data on bird species richness and abundance were collected visually and audibly using standardized 10-minute fixed-time point counts (Bibby et al. 2000), of 50-m radius, along each of the transects. While more accurate estimates of biodiversity can be obtained by taking into account detection probability (Buckland et al. 2008), our sampling methodology was chosen to match the sampling scheme of bird studies in the PREDICTS database. Because detectability is likely to be higher in more open habitats, which are often those with higher human land-use activity, our estimates of the effects of human land use on biodiversity (from both the broad-scale and independent datasets) are likely to be conservative. Point counts (N=147) were located along

the two transects to represent the land uses in the broad-scale dataset, and were visited twice between March and May 2014. Sites were spread across a wide elevational range in both transects (836-2142 m on Taita and 715-1735 m on Kilimanjaro). Some land use types could only be sampled in particular elevational ranges. For example, primary vegetation only occurs in high elevations on both transects (Figure 1, Figure S4-D). Our survey captured local diversity with total sampling effort comparable to similar studies in the broad-scale dataset (24 hours on Kilimanjaro and 25 hours on Taita Hills, compared with an average of 35.15 ± 15.92 (SD) sampling hours in the broad-scale dataset). Seasonal changes in the abundance of certain bird species might introduce bias into our field study; however, a resurvey of parts of the sites in a different climatic season showed similar responses of avian diversity to land use (Norfolk et al. in press). Species identity was determined following commonly used visual taxonomic guides and assisted by audio recordings from freely available bird-sound databases (Stevenson and Fanshawe 2004; <http://www.xeno-canto.org>). In total, 172 different bird species were observed at 147 locations in the two study transects. All sites were classified into the same land uses and land-use intensity as in the broad-scale dataset: primary vegetation (39 sites), secondary vegetation (31), plantation forest (27), cropland (69) and urban (14); and within these land uses, minimal, light and intense use-intensity. In the analyses, we treated the Kilimanjaro (74 sites) and Taita Hills (73 sites) transects as independent field studies owing to their distance from each other (~100km) and different geological and evolutionary history.

121

122 *Environmental and assemblage-structure data*

We tested whether site-specific variation in land-use intensity, human population density, forest cover and metrics describing vegetation greenness and vegetation removal mediate local responses to land use in the independent data compared with the broad-scale model estimates. We focussed on those variables because previous broad-scale models have highlighted their importance for biodiversity (e.g. Newbold et al. 2014a) and because they are readily available. We extracted forest cover in the year 2000 (the most recent year for which percent forest cover estimates are available at a fine scale) from recently published remote-sensing data at 30-m resolution (Hansen et al. 2013). For vegetation greenness and vegetation removal measures, we extracted data from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13Q1 product (the Normalized Difference Vegetation Index; NDVI) at 250-m resolution. Vegetation removal was estimated by calculating the area under the curve of a linear interpolation of NDVI over the three years prior to and including the year of the study following a method first suggested by Tucker et al. (1981), and adjusted for differences in climate seasonality (Newbold et al. 2014a). Mean NDVI over the same time span was used as a measure of average vegetation greenness, to represent continuous gradients of vegetation density not captured by the forest cover dataset. We chose NDVI as our vegetation indicator (rather than, for example, the Enhanced Vegetation Index) for comparability with

136 previous models (Newbold et al. 2014a). For human population, we used Africa-wide high-resolution (100-m) population
137 density (people per km²) estimates for the year 2010 (adjusted to match UN national estimates) from the
138 www.worldpop.org.uk datasets (Linard et al. 2012). Finally, we included local estimates of elevation from the Shuttle
139 Radar Topography Mission (SRTM) at 90-m resolution (Jarvis et al. 2008).

140 We investigated the range of species' characteristics within assemblages in both the Africa-wide dataset and the
141 independent sites, because these characteristics can influence responses to land use (Owens and Bennett 2000; Flynn et
142 al. 2009; Newbold et al. 2013; De Palma et al. 2015) and thus might mediate the effect of land use on biodiversity locally.
143 Due to the limited coverage and biased data on non-vertebrate species in publicly available databases, we limited this
144 comparison to avian species in both datasets. The analysis was further restricted to records in the assemblage data that
145 were determined to species level (98.4% of records), and matched to scientific names in the catalogue of life
146 (<http://catalogueoflife.org/>, see Hudson et al. 2014). In this analysis we focus on ecological rather than morphological
147 characteristics as for many of the African bird species in our analysis morphological traits are still unavailable. We
148 calculated assemblages' average geographic range size, habitat specialization and IUCN threat status. To estimate range
149 size, we calculated the log-transformed total area of bird species' extent-of-occurrence range maps (Birdlife International
150 2012), after first converting the range map to a 1° grid and restricting it to the continent of Africa. Range size were log-
151 transformed after visual exploration of the data revealed a strong right-skew of range sizes. The current IUCN threat status
152 for each species was obtained using an automatic query of the IUCN web-api (<http://api.iucnredlist.org/>; accessed
153 05/11/2014). We grouped all species with threat categories CR (Critically endangered), EN (Endangered) and VU
154 (Vulnerable) as threatened species, and species currently assessed as NT (Near threatened) and LC (Least concern) as
155 non-threatened; species classified as NE (Not evaluated) or DD (Data deficient) were not included further in the analysis.
156 IUCN threat was included owing to its high relevance to policy and decision makers. Finally, we downloaded information
157 on species' habitat preferences from IUCN to assess the percentage of individuals in assemblages that are forest
158 specialists, defined as those species for which any kind of forest habitat is considered to be of major importance. For each
159 site, we calculated, for all occurring bird species: 1) the average log-transformed range size; and the proportion of 2)
160 forest specialist species; and 3) threatened bird species.

161

162 *Data analysis*

163 For each site and dataset, we calculated two biodiversity metrics: species richness as the number of unique observed
164 taxa; and total species abundance as the sum of the abundances of all taxa (corrected where there was varying sampling
165 effort within the published studies, Newbold et al. 2014a). We first modelled the impact of land use with the broad-scale

166 data, using generalized linear mixed-effects models (GLMMs: Bolker et al. 2009), with a Gaussian distribution of errors
 167 for log-transformed abundance values and a Poisson distribution for species richness. The use of GLMMs was
 168 necessary to account for differences among studies (e.g. differences in sampling methods, sampling effort and
 169 taxonomic group sampled). These differences were accounted for by including the study identity as a random intercept.
 170 We tested if inclusion of taxonomic grouping as a random intercept improved the model (lower Akaike's information
 171 criterion – AIC); it did not. We also tested whether two other random terms improved model fit: 1) any spatial block of
 172 sampled sites, such as point counts along transects; and 2) land use as a random slope nested within study. For both
 173 models, the best random-effects structure (lowest AIC) contained a random slope of land use nested within study, and a
 174 random intercept for study identity. Initial models were constructed using the recorded land-use category as a single
 175 explanatory variable. Average species richness and total abundance in different land uses in the independent data were
 176 then compared with the coefficients of the land-use-only broad-scale model, with correspondence assessed using Z-
 177 statistics (Cohen et al. 2013), defined as $Z = \frac{b_{independent} - b_{broad-scale}}{\sqrt{SEb_{independent}^2 + SEb_{broad-scale}^2}}$, where b equals the slope of the modelled effect
 178 and SEb its standard error. A z-score is a standardized measurement that quantifies the offset of one value from a
 179 normally distributed mean with values smaller than 1.96 generally indicating non-significant deviations (Cohen et al.
 180 2013). Because of study-level methodological differences we could only calculate relative biodiversity values. We used
 181 primary vegetation as a baseline for both datasets and calculated the percentage difference in each other land-use
 182 category. Some of the differences between the broad-scale model and independent data might be because the
 183 independent data focused only on birds. To assess the extent to which this was the case, we also developed a broad-scale
 184 model with the same structure but only containing bird data from the broad-scale database (1090 sites).

185 To test whether the addition of more environmental information than just land use could improve the
 186 correspondence between the independent data and the broad-scale model, we developed a second set of GLMMs of
 187 species richness and total abundance using the broad-scale dataset. In these models we again fitted land use, but this time
 188 also land-use intensity (including in interaction with land use) and all continuous environmental variables (see above).
 189 We subjected this model to a model-selection process, by fitting models with all possible additive combinations of
 190 explanatory variables and selecting the model with the lowest AIC value. The goodness of fit (AIC and R^2 , assessed
 191 against the model-training data) of the new model and the land-use-only model were compared, and we assessed the
 192 importance of the included covariates by summing the AIC weights of all models containing each variable (Burnham &
 193 Anderson, 2002). To assess the change in correspondence with the independent data both the best-performing model and
 194 a land-use-only model were used to predict abundance and species richness at the independent field-study sites, using the
 195 environmental variables.

196 We tested the residuals of both the land-use-only and the overall best-fitting model for spatial autocorrelation
197 using a Moran's I test. None of the individual studies showed significant autocorrelation within our models (SI Figure 2).
198 All analyses were performed in R (ver. 3.2.2, R Core Team 2014) mainly using lme4 (ver. 1.1.10, Bolker et al. 2009; Bates
199 et al. 2014) for model fitting, AICcmodavg for model selection (ver. 2.0.3, Mazerolle 2015), spdep for spatial
200 autocorrelation tests (ver. 0.5-88, Bivand and Piras 2015) and MODISTools (ver. 0.94.6, Tuck et al. 2014) for obtaining
201 NDVI data.

202

203 **Results**

204 Responses to land use of both biodiversity metrics were largely consistent between the modelled broad-scale
205 estimates and the independent data, although there were large discrepancies for some land uses (Figure 2; log-abundance:
206 median absolute $Z = 0.991$, range = 0.06 – 5.76, species richness: median absolute $Z = 0.728$, range = 0.037 – 2.877).
207 The biggest discrepancy between the independent data and broad-scale model was for cropland sites: the independent
208 sites (especially in the Taita Hills transect) had much higher total abundance and species richness than predicted from the
209 Africa-wide dataset (Figure 2). This discrepancy became smaller for abundance if the broad-scale model was based only
210 on bird data, but this was not the case for the species richness model (SI Figure 3). There was large uncertainty around
211 the means, especially in the broad-scale dataset, reflecting a wide range of responses among different studies (SI Figure
212 1).

213 There were considerable differences in local environmental conditions between the Africa-wide and independent
214 field datasets (Figure 3). Mean vegetation greenness (NDVI) of independent sites in primary vegetation, secondary
215 vegetation and plantation forest were lower than the average African site, whereas the opposite was true for cropland and
216 urban sites in the Taita hills. Forest cover was higher in primary vegetation and cropland at sites on both independent
217 transects. Independent sites had a higher human population density than the average African sites in all land-use
218 categories, especially urban sites, which had up to 2.5 to 4 times higher density than the African-wide average (Figure 3).

219 The full model based on the broad-scale dataset, and including all environmental variables as explanatory
220 variables, showed a better fit to the data for both total abundance ($\Delta AIC = 1591.91$, $\Delta r^2_{GLMM} = 0.08$) and species richness
221 ($\Delta AIC = 4562.48$, $\Delta r^2_{GLMM} = 0.02$). However, these models still only explained a low proportion of the observed variation
222 in total abundance (marginal $r^2_{GLMM} = 0.09$) and species richness ($r^2_{GLMM} = 0.03$). Across all candidate models, land use,
223 land-use intensity, their interaction, and vegetation removal were of the greatest relative importance for explaining
224 abundance and species richness (for each of these variables, summed AIC weights, $\sum AIC_w \approx 1$). Human population
225 density was of high importance for species richness ($\sum AIC_w \approx 1$), but less important for abundance ($\sum AIC_w = 0.589$).

Mean vegetation greenness of the three years before the sampling was more important for abundance ($\sum AIC_w = 0.944$) than for species richness ($\sum AIC_w = 0.506$). Elevation was not selected among the explanatory variables in the best model, and was of lower importance for both species richness ($\sum AIC_w = 0.270$) and abundance ($\sum AIC_w = 0.316$). Furthermore, elevation did not show a significant correlation with species richness ($p > 0.05$) at the independent field sites. However the abundance of bird species in the Taita hills decreased significantly with increasing elevation ($P < 0.001$, Figure S4-B). We found the difference between model-predicted values and observed values in the independent data to be quite mixed depending on the model used, the biodiversity metric considered, and the land use in question (Figure 4). For abundance the land-use-only model (average absolute difference = 19.81%) performed slightly worse in predicting relative abundance compared to the best selected model (average absolute difference = 18.83%), while for species richness the land-use-only model predictions were closer to the observed (average absolute difference = 15.47%) than those from the best selected model (average absolute difference = 27.44%). A notable exception was cropland, for which the predictions made by the full model with all environmental factors were substantially better than those made by the land-use only model (Figure 4).

Bird species at our independent sites were on average more wide-ranged species compared to bird species at sites in the broad-scale dataset (Figure 5), with the exception of primary forests in the Taita hills, where significantly more narrow-ranged species were found. Sites in the independent dataset had similar or lower proportions of forest specialist species than the sites in the broad-scale dataset, with the exception of primary vegetation and cropland in the Taita Hills where the proportion of forest specialist birds was higher (Figure 5). Our independent sites had similar proportions of threatened bird species as the average site in the broad-scale dataset, but higher proportions in primary vegetation in the Taita Hills study area (Figure 5).

Discussion

Our results show that independently observed local biodiversity responses to land use are mostly consistent with broad-scale model estimates. While species richness consistently declines with increasing levels of human land use in most cases (Figure 2), the total abundance stays fairly stable. However, the broad-scale model showed that responses to land use vary substantially among different studies (Figure S1); this heterogeneity is especially apparent in urban sites, perhaps because local factors, such as vegetation greenness and proximity to nearby forests, mediate responses. It should be noted however that there are only few urban studies in Africa in the database, indicating that there is a need for further research on the effect of urbanization on biodiversity in this continent. We could not detect any influence of elevation on species richness in either of our independent sites or the broad-scale dataset. However, bird abundance decreased with

elevation in the Taita hills, which could be explained by the fact that the low elevation areas receive many nutrients and water, thus increasing resources and diversity of land cover available for many bird species. Similarity of species composition decreased with increasing elevational distance between sites (Figure S4-C), thus indicating a turnover of species assemblages with elevation. Land use has likely added to this effect and might have altered the natural elevational gradient in species richness (McCain 2009). The interaction between elevation and land use however could not be tested with confidence as land use in both study transects is not spread equally across elevations (Figure S4-D). In particular, primary vegetation sites are significantly higher in elevation than other land uses (see next section for possible implications of this for the results). The biggest discrepancy between the biodiversity estimates was for cropland: the independent data had higher values of both biodiversity metrics than predicted from the Africa-wide dataset. This might partly reflect the fact that the field survey sampled only birds: bird-only models of the broad-scale datasets decreased the mismatch within cropland, at least for abundance (SI Figure 3). Previous research has shown that taxonomic groups can show different responses to land use (Lawton et al. 1998; Schulze et al. 2004; Newbold et al. 2014a). Birds are highly mobile species, often dependent on various habitats in the surrounding landscape (Haslem and Bennett 2008) and show seasonal fluctuations of activity. Therefore our independent field data will reflect neither the whole assemblage present in the study area nor the general effect of land use on biodiversity. The discrepancy emphasizes the need to collect field data for a set of taxonomic groups that are as representative as possible. In addition to real taxonomic differences in responses to land use, it is likely also that surveying of different taxonomic groups is done at different spatial scales, which could also cause apparent differences in responses among taxa (note however that a previous study using the same dataset found little effect of sampling scale on relative differences in diversity among land uses; Newbold et al. 2015). On the other hand, the broad-scale model omits several aspects of the local environmental and ecological conditions, which we discuss in the following sections.

Impoverished species pool

One explanation for the difference in biodiversity between cropland sites on the Taita Hills and the average cropland site in the Africa-wide model could be that the primary vegetation in Taita Hills has already suffered more biodiversity loss than the average primary-vegetation site in the broad-scale dataset. The Taita Hills have a high degree of habitat fragmentation and the lowest overall forest cover in all of the Eastern Arc Mountains (Newmark 1998; Platts et al. 2011), reflecting the long history of human modification and disturbance in the area (Newmark 1998; Brooks et al. 1998; Heckmann et al. 2014). Such conditions might have influenced the response of species richness to land use by leaving assemblages that are impoverished and relatively insensitive to further land-use disturbance (Filippi-Codaccioni

et al. 2010); the resulting biota might also show different associations between species characteristics and sensitivity than seen in newly impacted regions (Fritz et al. 2009).

The greater Kilimanjaro area and the Taita Hills have been used by humans for many centuries (Heckmann et al. 2014). Expeditions undertaken by German missionaries visiting Mount Kilimanjaro noted that the land was already extensively used in the 19th century (Börjeson 2009) and similar evidence suggests that the agricultural terraces of the Taita Hills are centuries old (Conte 2010). These sources indicate that most of today's natural vegetation was cleared by pre-modern settlers, posing the question of whether the current remaining natural vegetation can truly be called 'primary vegetation' (Willis and Birks 2006). The loss of natural vegetation seems to have accelerated in the last century owing to increasing human population density, colonial forestry operations (Brooks et al. 1998; Burgess et al. 2007b; Platts et al. 2011) and the ongoing shift from traditional forms of crop cultivation to monoculture farming (Soini 2005; Hemp 2006b). Broad-scale models would benefit from incorporating estimates of land-use history, but the currently available data (e.g. Klein Goldewijk et al. 2011) are too coarsely resolved to be very useful.

Our study sites had on average a similar proportion of forest-dependent species in primary vegetation, but a smaller proportion in plantation forest sites than in the broad-scale dataset (Figure 5). However, the average number of narrow-ranged and threatened bird species was higher on the Taita hills compared to sites across Africa, which reflects the high conservation value of large continuous forest in this global biodiversity hotspot (Burgess et al. 2007b), and suggests that not all sensitive species have yet been lost from assemblages at the Taita hills. It has been suggested that plantation forests could support conservation efforts if appropriately managed (Brockerhoff et al. 2008). However, this does not seem to be the case for our field sites: plantation forests, such as *Eucalyptus*, pine and *Cypress* stands on Taita Hills had lower abundance and species richness than either primary or secondary vegetation (Figure 2), emphasizing the importance of natural vegetation for local biodiversity conservation (Brooks et al. 1998; Farwig et al. 2008; Gibson et al. 2011). Overall, our results support evidence (Owens and Bennett 2000; Flynn et al. 2009; Newbold et al. 2013; De Palma et al. 2015) that accounting for functional characteristics can add precision to broad-scale biodiversity models for certain well-studied taxonomic groups.

It is also possible that the species pool appears impoverished because the reference primary vegetation sites were located at high elevations, which are probably less diverse naturally. However, this is unlikely to explain our results entirely for three reasons. First, cropland had relatively high biodiversity even when compared with secondary vegetation, which like cropland was found at lower elevations in our field study areas. Second, other human land uses didn't have as high biodiversity as cropland despite also being found at low elevations. Third, the observed mismatch in biodiversity in croplands can be best explained by the occurrence of low-intensity agroforestry systems (known locally as 'homegardens'), which were located at higher elevations than more intensively used croplands.

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High-diversity cropland

Cropland sites in our independent dataset had relatively high diversity and a possible reason could be the management mode, since the majority of these sites were tropical agroforestry systems known locally as ‘*homegardens*’, which occur in mid-high elevational ranges. Tropical homegardens, such as the Chagga homegardens on Kilimanjaro, have many biodiversity-beneficial characteristics of agroforestry systems such as higher indigenous tree density and permanent or semi-permanent cultivation cycles, thus ensuring consistent vegetation cover and provision of valuable microhabitats (Hemp 2006a; Scales and Marsden 2008; Jose 2009). They can thus contribute to the persistence of species in human-modified landscapes (Bhagwat et al. 2008; Kabir and Webb 2008; Gardner et al. 2009), a conclusion which our study supports. The landscape context and proximity to nearby remaining forest fragments could also have led to an increase in species richness.

We show that the cropland sites in our independent dataset have slightly higher forest cover and mean vegetation greenness than the typical cropland site in Africa (Figure 3). These environmental factors might help explain the discrepancies in estimated avian diversity, and led to better predictions of bird diversity in croplands when included in the models (Figure 4). We suggest that more research on broad-scale environmental variables that are locally relevant is needed to improve models of biodiversity responses to land use. In addition to differences in environmental variables, along both independent study transects, cropland sites were composed of slightly more forest-dependent species than the average cropland site in Africa, showing that the local environmental features of cropland are associated with retention of at least some forest species. We suggest that agricultural management practices and land-use dynamics are important factors to consider in broad-scale biodiversity models, either by considering the intensity of human land use (Newbold et al. 2015), explicitly recognising agroforestry as distinct land-use type (Alkemade et al. 2009), or by including remote-sensed information on vegetation greenness or tree cover in cropland (Pettorelli et al. 2005; Hansen et al. 2013; Newbold et al. 2014a).

Conclusion

We identified important local factors that mediate biodiversity's response to land use. Broad-scale models might be inaccurate if used to predict land-use impacts on biodiversity at local scales if local conditions do not conform to the average conditions seen in the broad-scale dataset. This highlights the importance of local surveys that identify the local conditions and influencing variables before applying generalized broad-scale models in a local context. On the other hand, field data sets need to consider a wide, representative set of taxa in order to be representative of biodiversity's response

347 to land use. The inclusion of local land management information, vegetation data from remote sensing, and species
348 characteristics information can make broad-scale models more applicable to local settings.

349

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495

Table 1: Best-fit model from among those using all possible combinations of explanatory variables for the broad-scale dataset. Pseudo-R² values were computed following (Nakagawa and Schielzeth 2013).

Model terms	Model	K	AIC	Δ AIC	LogLik	DF (resid)	R ² (marginal)	R ² (conditional)
Land use*Land use intensity + log(Population density) + Vegetation removal + mean Vegetation greenness	log-Abundance	34	3844.27	0	-1888.13	1515	0.088	0.876
Land use ~1		22	5436.18	1591.91	-2696.09	2224	0.009	0.879
		18	5440.37	1596.1	-2702.18			
Land use * Land use intensity + log(Population density) + Vegetation removal + Forest cover + mean Vegetation greenness	Species richness	35	10920.67	0	-5425.34	1984	0.034	0.926
Land use ~1		22	15483.15	4562.48	-7719.58	2834	0.013	0.919
		18	15484.08	4563.41	-7724.04			

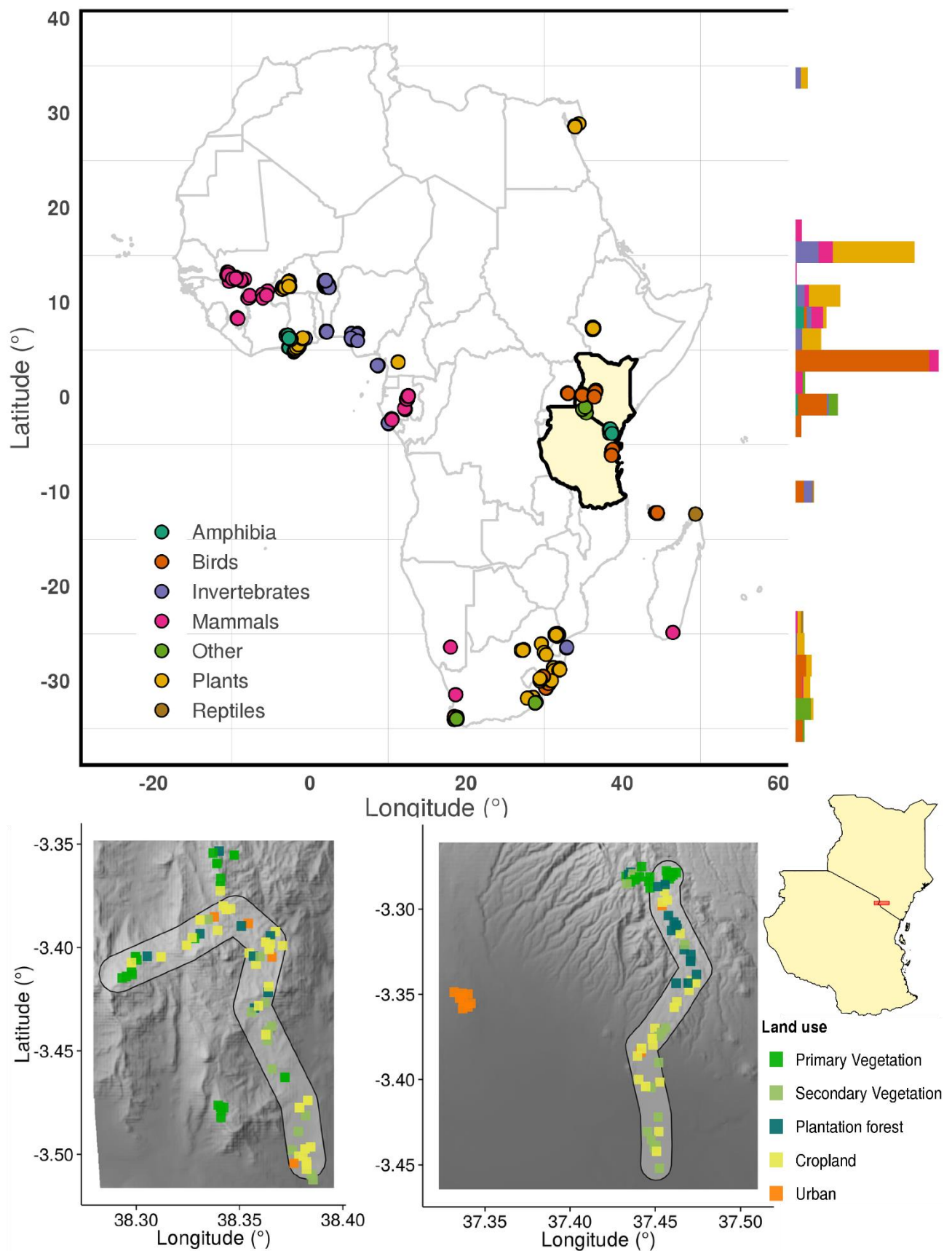


Figure 1: Distribution of broad-scale studies across Africa coloured by taxonomic group. Bars show the number of sites per latitude coloured by taxonomic group. Highlighted countries indicate the location of the independent field study transects, which consisted of sampling sites along two transects near Mount Kilimanjaro (left) and the Taita Hills (right). All sites are coloured by land use. The background to the panels showing the field transects is a hillshade model derived from SRTM 90m indicating the topographic relief of the sites.

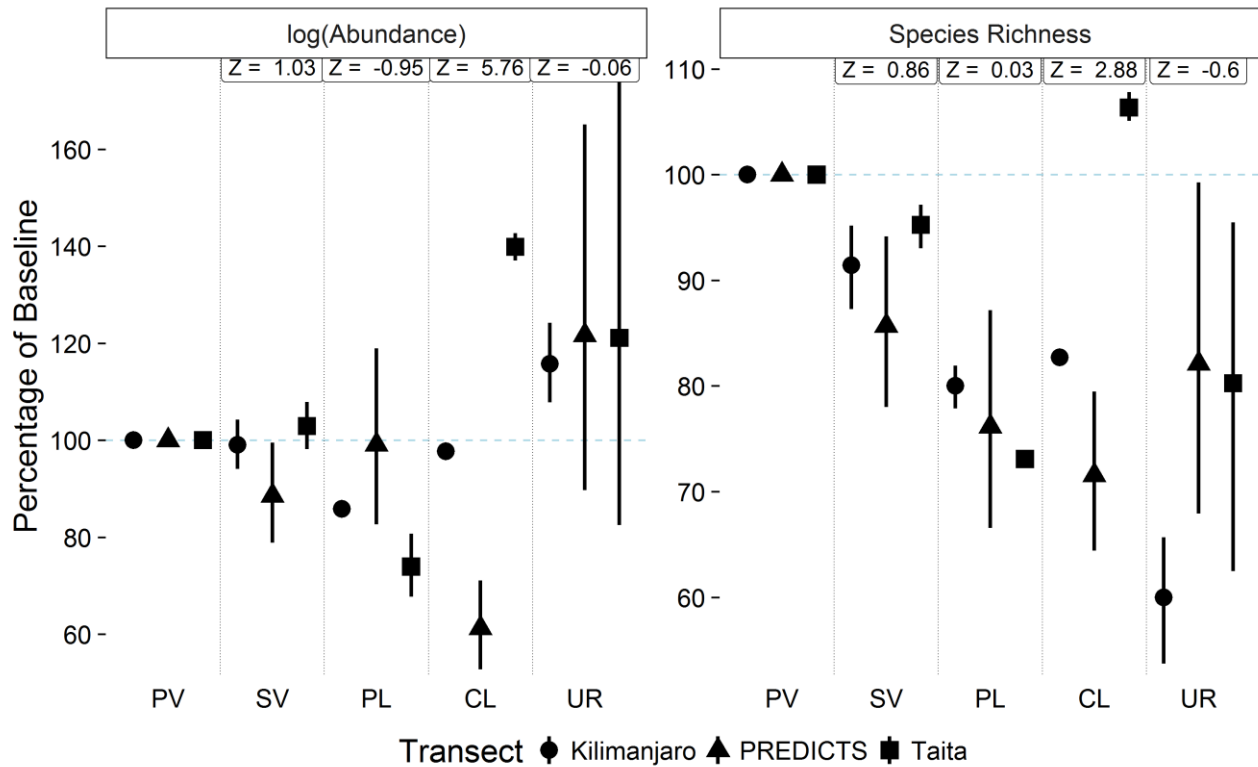


Figure 2: The response of species richness and total abundance to land use, from the Africa-wide model and the independent field data. Land-use categories are primary vegetation (PV), secondary vegetation (SV), plantation forest (PL), cropland (CL) and urban (UR). All coefficients are visualized as proportional difference to primary vegetation (PV), which was set at a baseline of 100%. Error bars show one standard error. Labels on top show the Z-statistic, which quantifies the distance between the independent data and the broad-scale modelled estimates, taking into account the uncertainty in both cases. Z-statistics further from zero indicate greater mismatch.

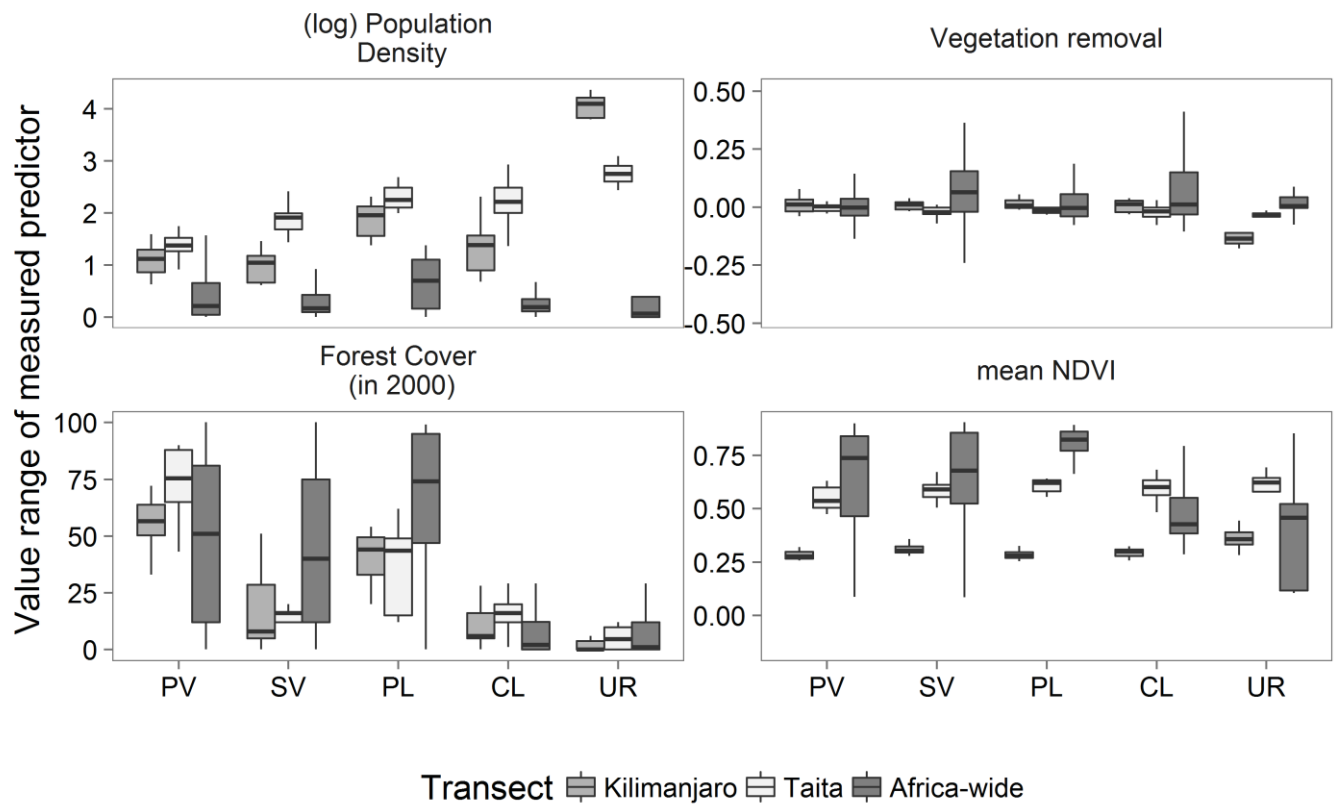


Figure 3: Difference in environmental variables in different land uses, between the broad-scale ('Africa-wide') and the independent field data ('Kilimanjaro' and 'Taita'). Boxes show the inter-quartile range, while lines show the full range of the data (or 1.5 times the upper and lower quartiles if less extreme). Abbreviations as in Figure 2.

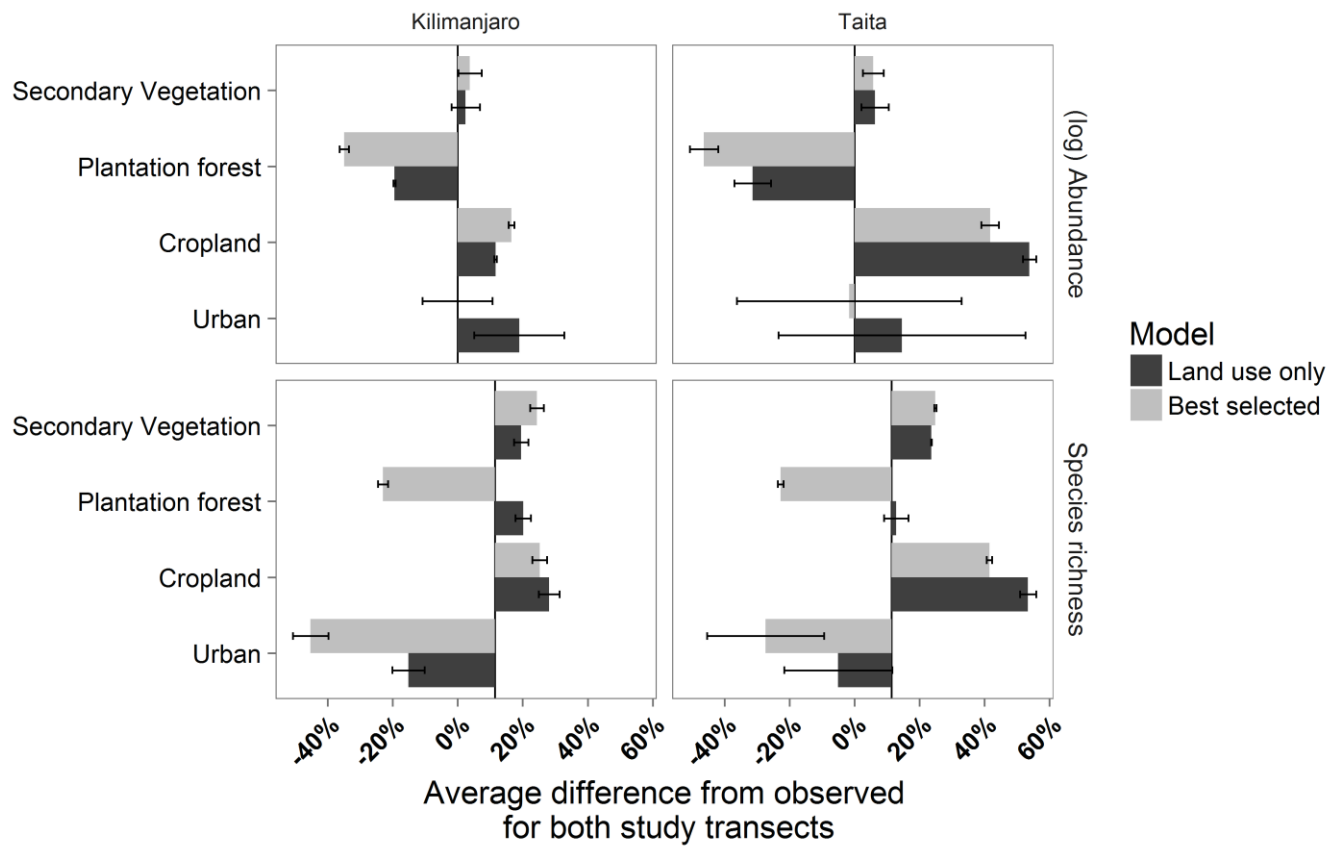


Figure 4: Difference between the relative observed biodiversity values at the field sites, and predicted biodiversity values from the best-selected model and a land-use-only model (see Table 1). Predicted values were obtained by applying the models to the estimated environmental covariates at the field study sites. The predicted model estimates were subtracted from the observed field values. Thus, positive values indicate a model predicting lower biodiversity than was observed with overall smaller bars indicating better fit to the observed. Primary vegetation was used as the baseline and abbreviations are as in Figure 2.

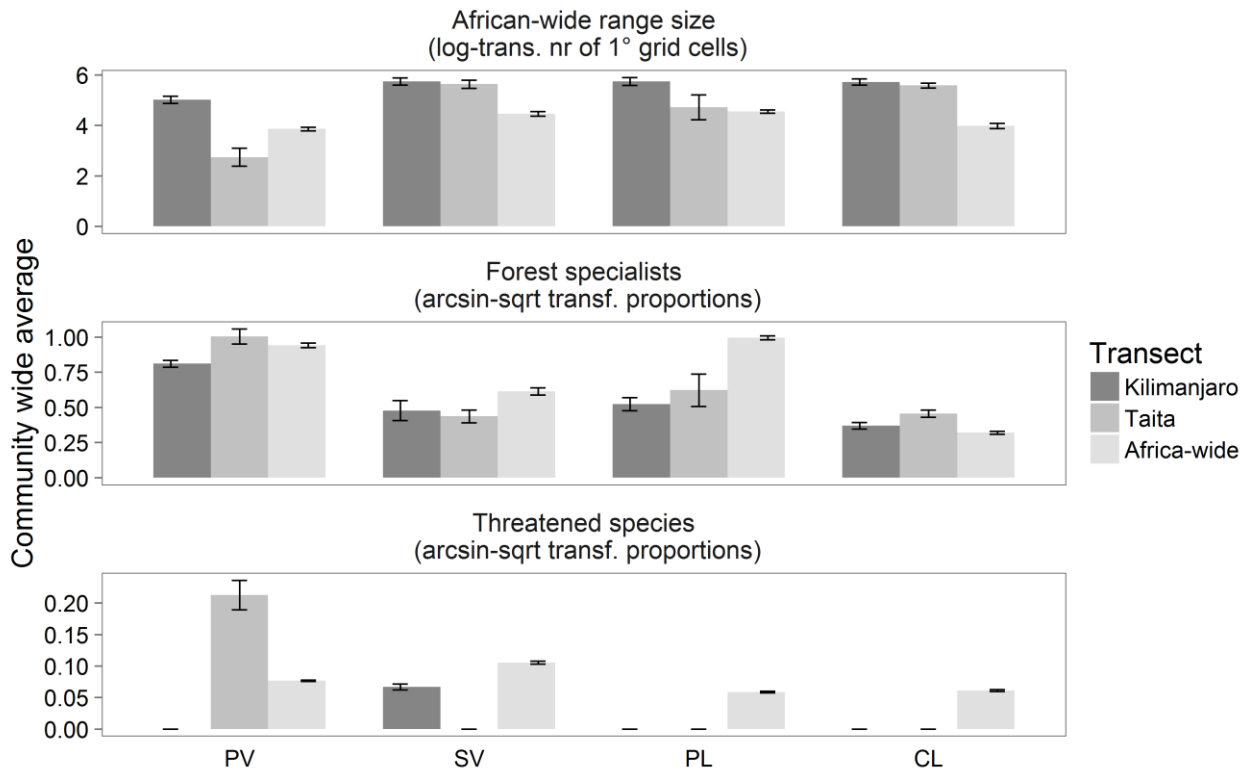


Figure 5: Average assemblage structure in terms of bird species' characteristics, for the broad-scale ('Africa-wide') and the independent ('Taita' and 'Kilimanjaro') datasets, in different land uses. Range size was measured as the average (log-transformed) extent of occurrence across Africa of all bird species recorded at each site, forest specialism was classified based on the IUCN classification of habitat preference, and threat status was from the IUCN Red List (species classified as critically endangered, endangered or vulnerable were considered to be 'threatened'). For each sites, we calculated the average proportions of species classified as forest specialist or as threatened. Proportions of forest specialist and threatened species was arcsin-squareroot transformed to better highlight differences. Error bars show the standard error of the mean.